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ORIGINAL ARTICLE

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The effect of airplane noise on frogs: a case study on the Critically Endangered Pickersgill's reed frog (*Hyperolius pickersgilli*)

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Abstract Species communicating acoustically may develop behavioral responses that aid them to transmit information and overcome signal masking in habitats disturbed by anthropogenic noise. Although many studies have concentrated on road traffic noise, very few studies mentioned effects of low flying airplane flyby noise on the vocal behavior of frogs. We studied the Critically Endangered Pickersgill's Reed frog (*Hyperolius pickersgilli*) native to the eastern coastal regions of South Africa as a case study. In order to evaluate the call of *H. pickersgilli*, we compared a site with high levels of airplane flyby noise to a reference site without any airplane activity. Our results show that *H. pickersgilli* males made changes in both temporal and spectral properties of their call. Males call significantly more during and after an airplane flyby in relation to the call rate before the noise stimulus, but resumed normal call rhythms when measurements were taken 15 min after overflight. We found that males call at higher mean dominant frequencies (df difference = 161.4 Hz, $P < 0.05$) when exposed to high-intensity airplane flyby noise. In comparison with call rate 5 min before the airplane flyby, males called 12 % more during and 18 % more after the airplane flyby. Although changes in the spectral and temporal properties of the call of *H. pickersgilli* were observed, this species was actively calling for much longer than any other local species. This is the first study from Africa to report effects of anthropogenic noise on anuran communication.

Keywords Airplane noise · Bioacoustics · Character displacement · Urbanization

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Introduction

Hearing plays an important role in enabling animals to find food, avoid predators, interact with con-specifics and recognize potential mates. The detrimental effect that anthropogenic noise has on animal communication systems in a variety of taxa are of growing concern (Landon et al. 2003; Barber et al. 2009a, 2009b; Popper and Hastings 2009; Dowling et al. 2012; Melcón et al. 2012). Studies have only recently begun to focus on the effect of noise on amphibian acoustic behavior (Boeckle et al. 2009; Kaiser and Hammers 2009; Parris et al. 2009; Cunnington and Fahrig 2010; Hoskin and Goosem 2010; Love and Bee 2010). While aircraft noise has been shown to have a significant effect on humans and wildlife (Pepper et al. 2003), surprisingly little research has been conducted on the effects of aircraft noise on anurans (Sun and Narins 2005).

The effectiveness of anuran communication and ultimately breeding success is not only subject to the discrimination of differences among signals by the receiver, but also the recognition of signals against background noise (Wiley and Richards 1978; Gerhardt 1982; Penna et al. 2005; Lengagne 2008; Wilkens et al. 2013). Increased urbanization gives rise to noisy environments that can have detrimental effects on anuran communication by masking acoustic signaling for mates (Sun and Narins 2005; Bee and Swanson 2007; Parris et al. 2009; Cunnington and Fahrig 2010; Vargas-Salinas et al. 2014). Effects of human-generated noise on anurans include: impaired sender and receiver detection thresholds and spatial orientation, reduction in breeding success, signal masking, changes in distribution, vocalization plasticity in temporal and spectral properties and sexual selection, i.e. female discrimination of males' calls (Wollerman 1999; Wollerman and Wiley 2002; Brumm and Slabbekoorn 2005; Bee and Swanson 2007; Eigenbrod et al. 2009; Fahrig and Rytwinski 2009; Parris et al. 2009; Cunnington and Fahrig 2010; Hoskin and Goosem 2010; Kaiser et al. 2010; Herrera-Montes and Aide

2011; Vargas-Salinas and Amézquita 2013). These effects, mostly produced by road traffic (vehicular) noise, have emerged as a field of interest and concern for many vocally active taxa, including anurans (Parris and McCarthy 2013; Vargas-Salinas et al. 2014).

Although most studies have concentrated on traffic noise, few have examined the effects of noise produced by low flying aircrafts on the call composition and behavior of frogs (Krause 2004; Sun and Narins 2005). Sun and Narins (2005) demonstrated that anthropogenic acoustic interference (either airplane flyby noise or motorcycle noise) may affect anuran chorus composition either by directly modifying call rate or indirectly by reducing calling in one species, thereby encouraging calling in others. Krause (2004) reported a case where Spade-foot toads (*Spea intermontanus*) lost their chorus synchronicity after a jet flew over the site and directly thereafter were preyed on by coyotes and a Great Horned Owl (*Bubo virginianus*).

This study describes the call characteristics of a population of *Hyperolius pickersgilli* at a site with minimal anthropogenic noise, and evaluates the effect of airplane noise on the temporal and spectral characteristics of the calls of this species at a site adjacent to a major airport. This is the first African study documenting the effects of anthropogenic noise on anuran communication and provides baseline data for future assessments of acoustic habitat degradation in other populations of this species.

Hyperolius pickersgilli is an elusive hyperoliid with a snout-vent length of less than 30 mm in females and 23 mm in males (Raw 1982; Du Preez and Carruthers 2009). Males emit soft, insect-like chirps from perches in dense reed beds, which may explain why this species was only recently discovered (Raw 1982). The IUCN lists this species as Critically Endangered due to its limited and severely fragmented global distribution. It occurs within a region that has been, and continues to be, heavily transformed by urban, agricultural and industrial development (IUCN 2014), and has therefore attracted conservation attention (Tarrant 2012; Tarrant and Armstrong 2013) and is the second anuran to require a Biodiversity Management Plan for Species (National Environmental Management: Biodiversity Act No. 10 of 2004; NEMBA 2004) in southern Africa. As with most temperate coastal anuran species, *H. pickersgilli* is active within the summer rainfall season that stretches from October through to February, when calling activity will decline as temperatures drop early March (Du Preez and Carruthers 2009).

Materials and methods

Study area

This study was conducted in a 7.19 ha wetland at Mount Moreland (29°38′16.87″S, 31°05′52.19″E), situated adjacent to King Shaka International Airport, KwaZulu-Natal, South Africa, and at Widenham, Umkomaas (30°13′02.07″S, 30°47′43.20″E), a reference site unaffected by airplane noise. One of the largest remaining populations of *Hyperolius pickersgilli* occurs at Mt Moreland. The Widenham wetland is situated in a quiet residential area and host a smaller population. Other frog species that breed at these wetlands include the Painted Reed Frog (*Hyperolius m. marmoratus*), Tinker Reed Frog (*H. tuberilinguis*), Bush Squeaker (*Arthroleptis wahlbergi*, a terrestrial breeder calling nearby the wetland), Natal Tree Frog (*Leptopelis natalensis*), Greater Leaf-folding Frog (*Afrixalus fornasinii*), Delicate Leaf-folding (*A. delicatus*), Natal Leaf-folding Frog (*A. s. spinifrons*) and Snoring Puddle Frog (*Phrynobatrachus natalensis*).

Monitoring chorus behavior

We set up two automated recorders (Song Meter, SM2 model, Wildlife Acoustics) at each of the two sites. The SM2 multidirectional microphones recorded at 16-bit full-spectrum on two channels and were set to record at 16 kHz sampling rate (90 dB signal to noise ratio). No filters were used for recordings. The Song Meter was set to record for 40 min per hour for 12 h, over seven nights at both sites (8–11 November 2012 and 18–20 February 2013). Recorders were placed approximately 10 m apart and were moved 10 meters deeper into the wetland to new positions each night in order to monitor different males. Up to eight males could be identified on recordings. However, only the two closest males (i.e. with the highest call amplitudes) were monitored to prevent double sampling (i.e. monitoring the same male twice). We monitored 10 and 20 males at Mt Moreland and Widenham, respectively. For each recording water and ambient temperature were continuously logged every five minutes by temperature sensors fitted to Song Meter SM2 recorders (Wildlife Acoustics).

Airplane flyby sound pressure levels

We also measured sound pressure levels (SPLs, Peak dB) of airplanes approaching the airport over the wetland (n = 22) and taking off in the direction of the wetland (n = 20). Sound pressure levels for airplane flyby noise were measured 1 m above the ground at angles of 30°, 45°, 90°, 135°, 150° as the airplane flew over. SPLs were measured (dB intervals, C-weighting) with a calibrated Brüel and Kjaer (calibration number: 2013-0285) precision sound-level meter (Model 2235) and microphone (Brüel and Kjaer 4176). Ambient noise levels for both sites were measured at 1 min intervals over 10 min on 11 November 2013.

Advertisement and aggressive call recording and description

In describing *H. pickersgilli*, Raw (1982) noted two types of calls, but did not distinguish them as advertisement or aggressive calls. Included in our study is the detailed description of both these calls. In addition to the passive acoustics recorders (Song Meters) used to monitor calling behavior, we collected directional digital recordings of the advertisement calls of *H. pickersgilli* using a Nagra ARES-ML digital recorder equipped with a Sennheiser ME66 microphone (44.1 kHz, 16 bit; frequency response = 40—20,000 Hz ±2.5 dB). We recorded six males from both Mt Moreland and Widenham in November 2012. The advertisement call is a soft pulsatile chirp produced by males. Call traits that were shown to be reliable for measurement of call variation in other studies (Gerhardt and Huber 2002; Hoskin 2004; Hoskin et al. 2005, 2009) were measured, including: call duration (length of call from beginning of the first pulse to end of the last pulse, ms), pulse rate (time elapsed from the beginning of the first pulse to the beginning of the last pulse, divided by the number of pulses between these two points), dominant frequency (frequency at which the call is of greatest intensity, Hz), call rate (number of calls per minute), inter-call interval (duration between the onset of successive calls, ms), bout duration (duration from the onset of the first call to the end of the last call before a conspicuous halt, ms) and number of pulses per call. Call duration, interval before next call, number of pulses per call, dominant frequency, bout duration and call rate were measured for the advertisement call; call duration and dominant frequency was measured for aggressive calls ($n = 2$) of two individuals using Song Scope (version 4.1.3A, Wildlife Acoustics). Air temperature was also logged by the Song Meter (1 m above water) with each recording (Table 1).

Due to the secretive nature of *H. pickersgilli* and the dense reed habitat we were not able to measure SPLs of the call in the field: these measurements were obtained from five captive males (n = 10) confined within a wire cage covered with thin stockings, set up on reeds within natural habitat at Mt Moreland. Sound pressure levels were measured at peak dB 300 mm away from the frog who was facing the sound level meter. Throughout all recordings measurements from analysis for call rate and the description of the call parameters were taken between 19:00 and 03:00 at peak chorus intensity.

Acoustic analysis

To analyze the vocal behavior of individual frogs during airplane flyby noise, calls emitted in the time periods 5 min before, during and 5 min after an airplane flyby were recorded on the Song Meters, and analyzed using Song Scope (v. 4.1.3A, Wildlife Acoustics). Frequency properties for calls at the Mt Moreland site were analyzed during periods when airplane noise was absent. Calling rate was calculated for each minute and call properties were analyzed. Sound spectrograms, oscillograms and power spectrums were generated using BatSound Sound Analysis (version 4.1.4, Pettersson Electronics and Acoustics).

Table 1 Summary of the call properties that were measured of six frogs from each of the sites; *N* refers to the number of calls analysed

	Mt Moreland ($N = 60$)	Widenham ($N = 60$)	Combined
Temperature (°C)			
Mean	18.5	14.7	16.6
Range	17.2–19.8	13.0–19.6	13.0–19.8
Standard deviation	0.7	1.4	1.3
Call duration (ms)			
Mean	161	159	160
Range	96–202	125–212	96–212
Standard deviation	27	19	24
Inter-call interval (s)			
Mean	4.1	3.4	3.8
Range	2.6–6.8	2.6–6.0	2.6–6.8
Standard deviation	0.9	0.7	0.9
Number of pulses per call			
Mean	5	5	5
Range	4–7	4–7	4–7
Standard deviation	0.7	0.6	0.7
Dominant frequency (Hz)			
Mean	3411	3162	3287
Range	3047–3730	2890–3573	2890–3730
Standard deviation	169	162	186
Bout duration (s)			
Mean	92.2	65.3	78.8
Range	60.0–111.4	46.6–138.8	46.6–138.8
Standard deviation	17.3	32.7	26.3
Call rate (calls m^{-1})			
Mean	15	17	16
Range	14–16	15–20	14–20
Standard deviation	0.8	1.8	1.7

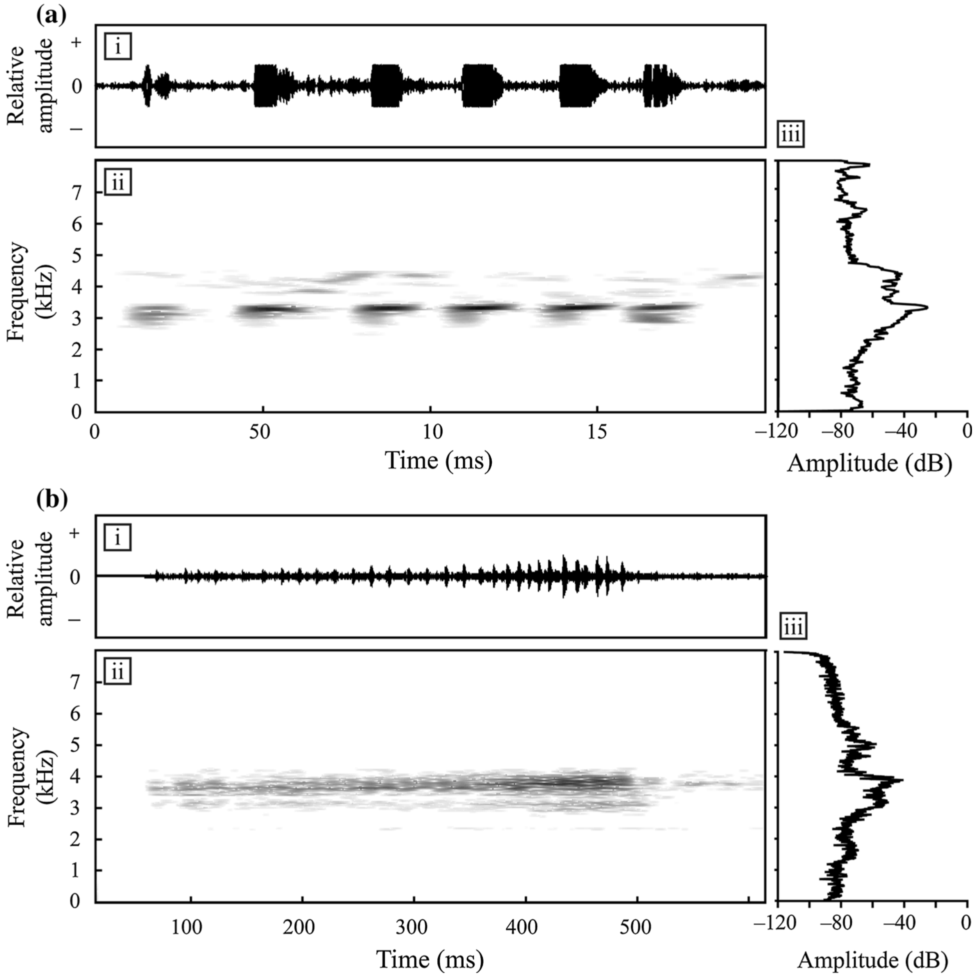

Fig. 1 **a** Advertisement call and **b** aggression call of *H. pickersgilli* with their respective oscillograms (*i*), spectrograms (*ii*) and power spectra (*iii*) recorded at 18.4 °C. FFT size for spectrograms = 1024, Hanning window

Statistical analysis

We used the independent samples *t* test to determine whether call frequencies and call rates differed significantly between the two sites. Differences were tested at 95 % confidence intervals. We used two-tailed Wilcoxon signed ranks test to determine statistical differences in call rate between pre-, during- and post airplane flyby noise. All statistical analyses were performed using SPSS 22.0 (SPSS IBM Corp 2013).

Results

Advertisement call and chorus structure of H. pickersgilli

Males typically prefer to call from level sections of vegetation being it folded leafs or fallen over *Phragmites* reeds about 100–700 mm above the water. Owing to the cryptic coloration of this species and the ventriloquial quality of its call, males are difficult to locate, even at short distances. Also calling males are very weary and would escape by diving into the water or disappearing into denser vegetation at the slightest disturbance. For this reason we were only able to catch two of the six recorded males to measure their snout-vent length. The two males' snout-vent lengths (SVLs) were 19.5 and 21.6 mm and the SPLs of these males were a mean of 80.2 dB (n = 10, 80.1–80.3 dB) and 82.3 dB (n = 10, 82.2–80.4 dB), respectively. Temperature ranged from 13.0 to 19.6 °C for all calls recorded at Widenham (Table 1).

The call comprises four to seven (usually five) pulses with dominant frequency (df) ranging from 2890–3573 Hz, n = 60, with an increase in pitch from the first to last pulse. Last pulses usually have noticeably lower amplitudes (Fig. 1a, Table 1). The call duration ranges from 125 to 212 ms. The pulsed aggressive call, df = 3374–3796, n = 2 (Fig. 1b, Table 2) has a lower mean dominant frequency as the added advertisement pulses (Table 2).

Males started calling between 18:00 and 19:00 (GMT +2:00) but most males were actively calling only after 19:00 reaching peak call activity around 01:00 am.

Table 2 Summary of the measurements of the aggression call from two males

	N	Temp. (°C)	Call duration (ms)		Dominant frequency (Hz)		Pulse dominant frequency (Hz)		Call type
			Mean	Range	Mean	Range	Mean	Range	
Subject 1	3	17.2	340	284–373	3461	3374–3539	3607	3562–3655	Aggression transition
Subject 2	5	18.5	449	434–465	3785	3775–3796	–	–	Aggression

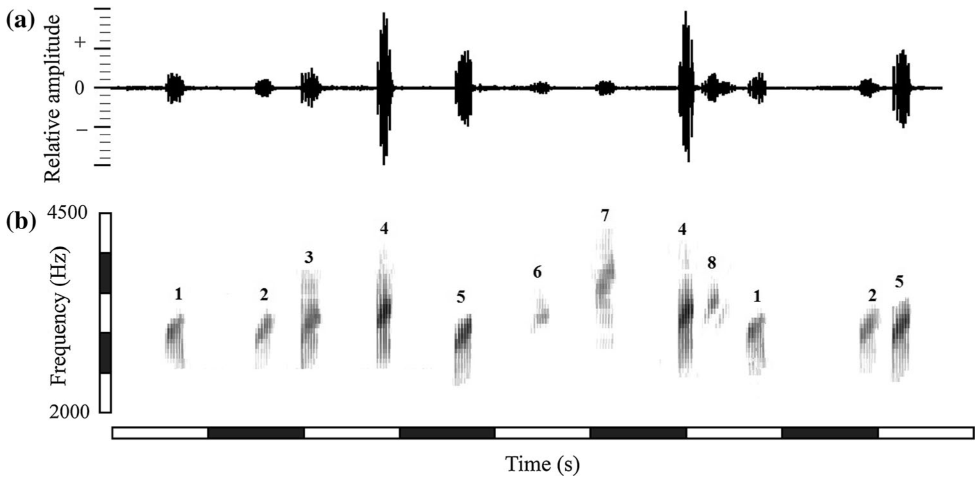

Fig. 2 An oscillogram (*top*) with associated spectrogram (*bottom*) of a typical *Hyperolius pickersgilli* chorus organization. Here we identified calls from eight males using the spectral properties in combination with the relative amplitude

Calling activity started to decrease from 05:00 and ceased before 06:00. Calling males were also heard at 10:00 am when sites were visited during daytime (J. Tarrant, pers. comm.). Concerning chorus organization, *H. pickersgilli* exhibits antiphonal calling, i.e. alternating calls with nearby rival males, calling from 15–20 times per minute (Fig. 2, Table 1).

Effects of airplane flyby noise on call temporal properties

Peak ambient SPLs ranged from 60.0 to 69.0 dB for Mt Moreland and from 62.1 to 69.8 dB for Widenham. Maximum SPLs ranged from 85.6 to 98.2 dB for landing aircraft and 88.2–91.7 dB for aircraft taking off over the wetland (Fig. 3). As can be expected different types of aircraft produce different noise levels. Airplane noise typically has harmonics at low frequencies, but also contains high power harmonics at frequencies up to approximately 1 000 Hz (Sun and Narins 2005). Ambient temperature at the time of measurement was 22.6 and 22.8 °C respectively for the times of take-offs and landings. Sound pressure levels for calls of *H. pickersgilli* males varied from 74.9 to 87.5 dB ($n = 30$, SVL 18.6–21.1 mm, 17.4 °C) for Mt Moreland specimens and 80–87.8 dB ($n = 20$, SVL 19.5–21.6 mm, 17.1 °C) for Widenham. SPLs were measured 300 mm from subjects.

Males exposed to high levels of airplane flyby noise called significantly more frequently than males at the reference site (Fig. 4a; Table 3). The mean call rate of 8.2 calls/minute, five minutes before airplane flyby, increased by 12 % during, and 18 % after the flyby (Fig. 4B; Wilcoxon signed-ranks test: during, $Z = -2.497$, $P = 0.013$; after, $Z = -2.059$, $P = 0.039$) whereas males at Widenham that averaged 6.2 calls/min during a 14 min recording, showed no statistical differences between 5, 4, and 5 min periods ($P > 0.05$; Fig. 4c). Males exposed to airplane flyby noise call at higher rates for longer periods (Fig. 5) during overflights as opposed to the normal cyclic call-rest rhythm of bouts lasting 2–5 min and resting periods of 1–3 min at Widenham (Fig. 6). However, when airplanes passed, males resumed their normal call-rest rhythm within a few minutes of absence of plane noise (Fig. 5). During the peak breeding season choruses can last at least 12 h on some nights.

Effects of airplane flyby noise on call spectral properties

Males exposed to low-flying airplane fly-by noise called at significantly higher dominant frequencies (3362.2 Hz; $P < 0.05$) than males from the reference site (3200.8 Hz; Table 3; Fig. 7). Not only were the dominant frequencies from males exposed to excessive airplane noise higher for every pulse of the call with

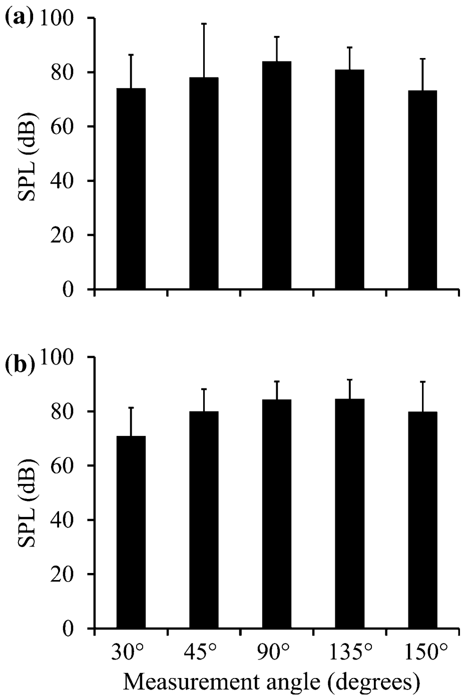

Fig. 3 Sound pressure levels (dB, Peak) of airplanes (**a**) coming into land (n = 22) and **b** taking off (n = 20) over the wetland situated in front of the airport. Measurements were taken by directing the sound level meter towards the airplanes' line of flight on the angles indicated by the x-axis

comparison to the calls of the males at Widenham, but the distribution of mean dominant frequencies of the pulses differ between controlled and exposed populations (Figs. 7, 8). Airplane activity gradually decreased after 19:00 with a single airplane flyby per hour around midnight (Fig. 9).

Discussion

This study provides evidence of *H. pickersgilli* males calling at higher pitches in the presence of high intensity airplane noise as well as momentary changes in temporal properties of their calls. Both airplane and traffic noise, e.g. motorcycle noise, occupy low frequencies (Sun and Narins 2005) and although most previous studies have focused on traffic noise (Kaiser and Hammers 2009; Parris et al. 2009; Cunnington and Fahrig 2010; Hoskin and Goosem 2010), noise from low-flying airplanes have unique power and frequency spectra. Low-flying airplane noise mask frog calls completely in power (i.e. intensity) for a number of seconds due to its high SPLs disrupting chorus structure and modifying call spectral and temporal properties (Krause 2004; Sun and Narins 2005; Parris et al. 2009). The physical environment may provide protection from anthropogenic noise by signal structure degradation and attenuation of sound due to spherical spreading of sound waves, atmospheric absorption and scattering (Michelsen 1978; Wiley and Richards 1978, 1982; Richards and Wiley 1980; Forrest 1994; Bradbury and Vehrencamp 1998; Ziegler et al. 2011). Reverberations are most severe in densely vegetated habitats (Wells 2007), as is the case of *H. pickersgilli*'s habitat. However, when sound is propagated directly from above, i.e. airplane noise, dense reedbeds provide little buffer from noise.

Effect of low-flying airplane flyby noise on spectral and temporal properties of calls

We observed an increase of 249 Hz in the mean values of the dominant frequency of *H. pickersgilli* calls when exposed to airplane noise. Whether this frequency shift affects mate choice by females in a noisy natural environment (Wollerman and Wiley 2002), is unknown for *H. pickersgilli* and in need of further studies. Noise can affect different species in diverse ways. One strategy anurans use to ensure successful communication in noisy environments is to reduce acoustic interference by temporal and spectral partitioning (Narins 1982; Drewry and Rand 1983; Gerhardt and Schwartz 1995; Garcia-Rutledge and Narins 2001; Sun and Narins 2005; Arch et al. 2009; Kaiser and Hammers 2009; Parris et al. 2009). However, since frog calls are innate rather than learned, there are substantial limitations to call plasticity in comparison to other vertebrate groups, i.e. birds (Rand 1985; Hauser 1996; Parris et al. 2009; Parris and Schneider 2009). Although plasticity in vocalizations of anurans allows them to maintain acoustic communication in the presence of traffic noise (Cunnington and Fahrig 2010), it is predicted that some frogs might take a minimum of 20 years to make larger frequency shifts (Parris et al. 2009). *Hyperolius pickersgilli* appears to avoid close proximity to *H. m. marmoratus* populations (Raw 1982; pers. observ.). Raw (1982) speculates that this spatial separation might be due to differences in the oxygen tolerances of the eggs of the two species. While this explanation is not excluded, we propose that the reason for this spatial distribution difference is to mitigate acoustic competition due to the overlap in the species advertisement calls. At the Mt Moreland study site the *H. marmoratus* population has moved into one pond area while *H. pickersgilli* concentrated more along the densely vegetated periphery of the pond, suggesting that airplane noise might influence competition between these species (J. Tarrant pers. comm.).

We found that when exposed to high intensity airplane flyby noise which masked their own calls, *H. pickersgilli* males increased calling effort during and after flyby stimuli relative to pre-stimulus call rates. Airplane noise may act directly by modulating the call rate of *H. pickersgilli*, or indirectly, by suppressing calling activity of heterospecific males, which in turn initiates calling in *H. pickersgilli* as exemplified in studies on other frog communities (Sun and Narins 2005; Kaiser and Hammers 2009). Although not acoustically analyzed in this study, a number of other species (see

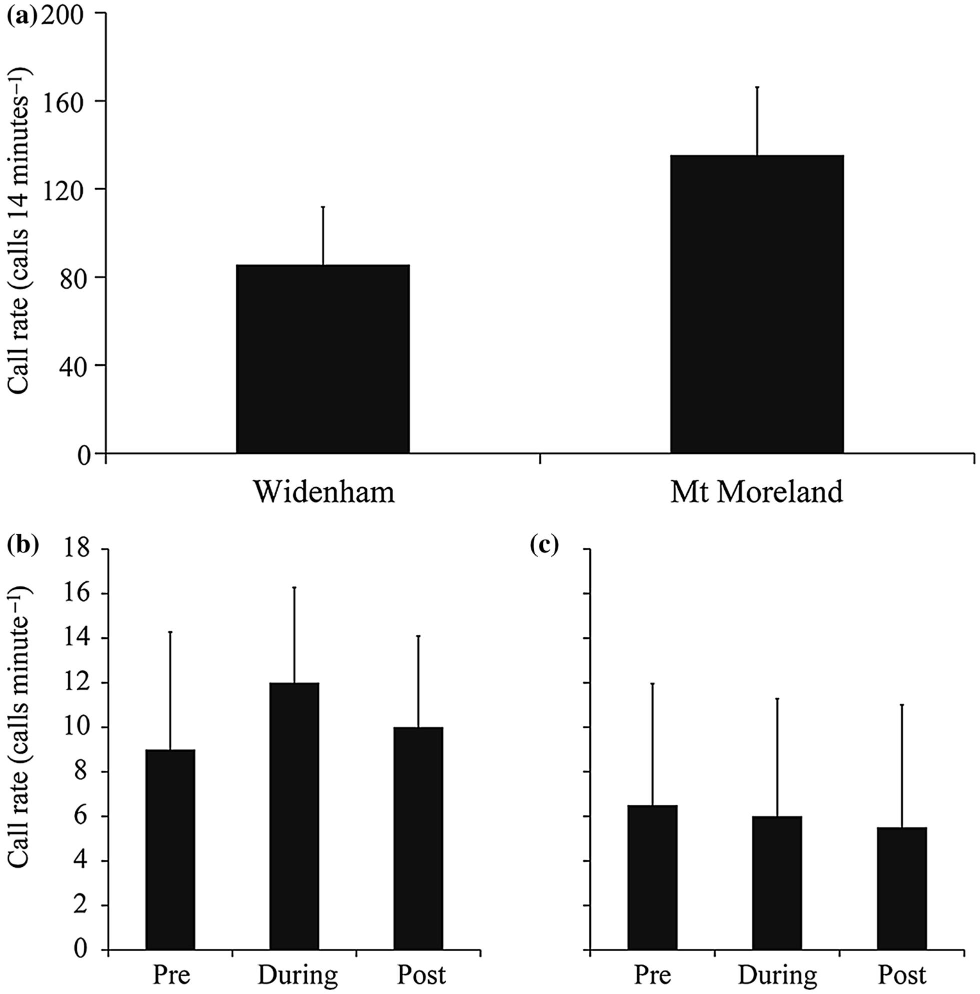

Fig. 4 **a** Call rates measured over a period of 14 min at the control site (Widenham, $n = 20$) and the experimental site with airplane flyby noise (Mt Moreland, $n = 10$). **b** Mean call rates from 10 males during 14 min recordings of 5 min before (Pre), 4 min from the onset (During) and 5 min after an airplane flyby (Post). **c** Call rate variation from 20 males over a period of 14 min divided into five (Pre), four (During) and five (Post) minutes. *Error bars* represent standard deviation

Table 3 Summary of t-test for equality of means for significance between call frequency and call duration of airplane flyby noise exposed males (Mt Moreland) versus non-exposed males (Widenham); 95 % confidence interval of the difference was used

	N	Mean	SD	SE	*t*-value	df	Sig. (2-tailed)
Dominant frequency* (Hz)							
Mt Moreland	60	3362.2	169.3	21.9	5.4	118.0	0.000
Widenham	60	3200.8	157.0	20.3	5.4	117.3	
Call rate* (calls min^{-1})							
Mt Moreland	10	135.3	30.9	9.8	–4.4	15.7	0.001
Widenham	20	85.6	26.2	5.9	–4.6	28.0	

* Ten calls from six males were analysed for each site, whereas call rate of 10 and 20 different individuals were measured for Mt Moreland and Widenham, respectively
df degrees of freedom

Materials and Methods) were identified at both sites during passive and active recording surveys. Although not statistically analyzed, there was visually (by means of chorus clusters in soundscapes) no apparent effect on the chorus activity of *H. marmoratus*, but *P. natalensis* avoided chorusing near events of airplane overflights.

Reproductive character displacement and anthropogenic noise

Spectral separation among members of an assemblage is a phenomenon that arises coincidentally, by means of selection on call spectra (perhaps to reduce acoustic

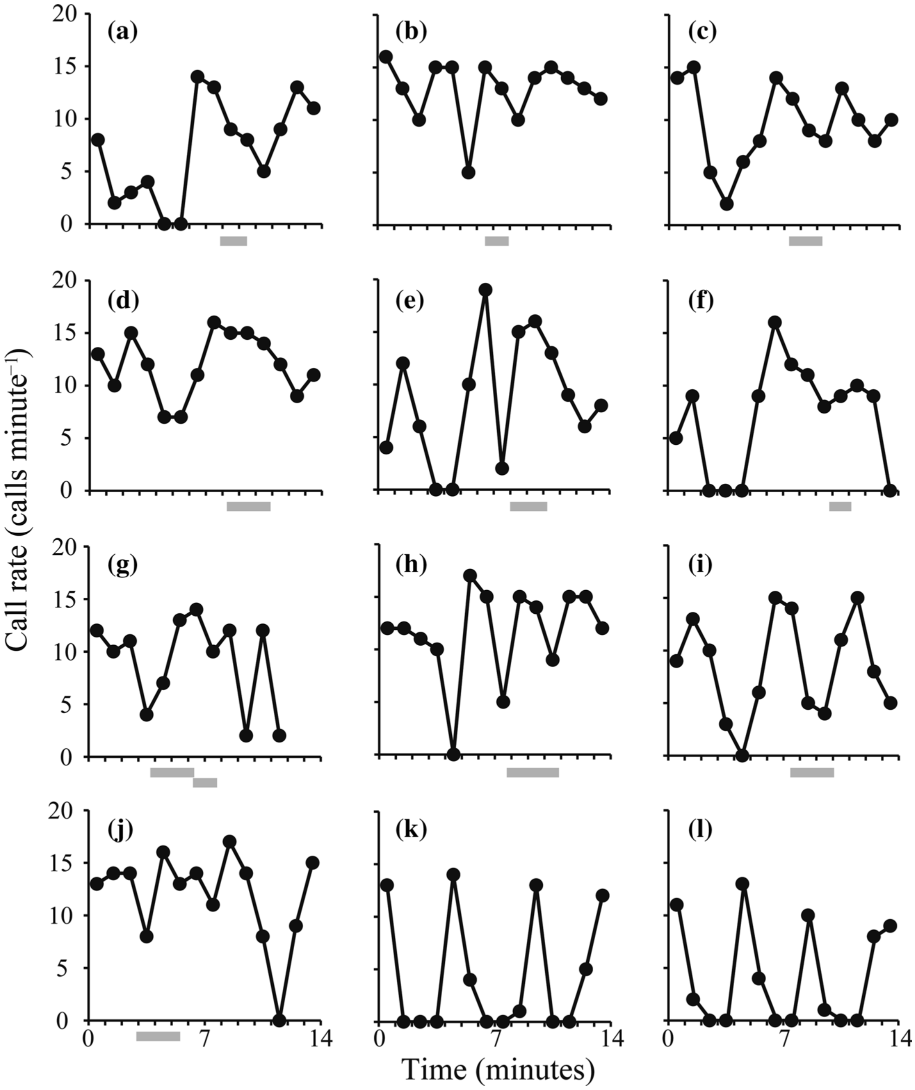

Fig. 5 Fourteen-minute call rate intervals of 10 *Hyperolius pickersgilli* males (**a**–**j**) in the presence of airplane overflights at Mt Moreland, with one instance of two airplanes overflights (**g**). K and *L* represents 14-min call rate intervals of males h and i 15 min after airplane overflights where call bouts assumed normal durations (see Fig. 6). *Grey bars* representing airplane flyby low-frequency noise duration

interference), or by providing a selective advantage to those species that join and remain in a chorus (Schwartz and Bee 2013). However, when two species of frogs with similar advertisement calls occur in sympatry, females might get confused with vocalizations and select heterospecific males. Subsequent hybrid offspring have lower fitness than offspring of conspecifics, resulting in selection to favor males with calls that are least similar to the other species. This divergence in call characteristics are known as reproductive character displacement or reinforcement and is usually reported on temporal properties of calls (Blair 1974; Gerhardt and Huber 2002). However, this mechanism might be true for *H. pickersgilli* in the spectral domain, where anthropogenic noise act as "the other species" creating competition in the acoustic habitat. Because maladaptive hybridization have to be present for the process to be defined as reinforcement (Hoskin et al. 2005), it cannot be named as such when the selection pressure originates from an external source. Males calling at a higher pitch may be favored by being more audible to females and thereby producing male offspring that also call at a higher pitch (Parris et al. 2009).

Implications for conservation due to a change in call properties and behavior

Male frog advertisement calls are one of the most energetically expensive activities reported for ectothermic vertebrates (Mac Nally 1981; Bucher et al. 1982; Taigen and Wells 1985; Taigen et al. 1985; Prestwich et al. 1989; Wells and Taigen 1989; Emerson 2001). Calling males experience energetic costs 10–25 times

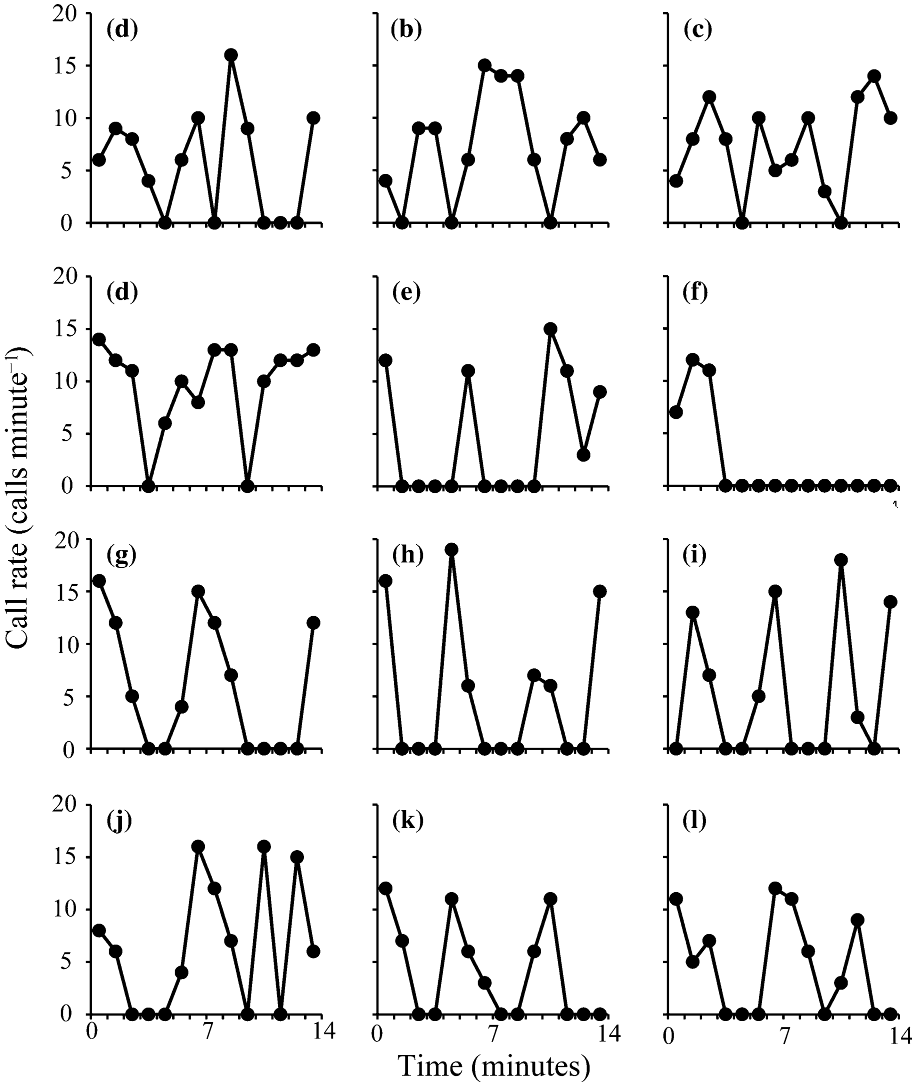

Fig. 6 Call rate of an individual *Hyperolius pickersgilli* male of the first recorded 14 min of each hour from 18:00–05:00 (*a–l*, respectively) at the control site, Widenham. This illustrates the typical cyclic rhythm where a male will rest between one and 4 min before continuing with the next bout

greater than that of resting individuals, with calling rate positively correlated to metabolic rate (Pough et al. 1992). Energy conservation tends to shape the strategy of calling in frogs (Schwartz and Gerhardt 1995; Grafe 1997). The observations from this study have implications for energy expenditure for males of *H. pickersgilli* at the test site due to the increased calling rate and absence of a resting phase between bouts in the presence of airplane noise. However, increased calling rates are only momentarily and airplane activity is lower in the evening.

Our results suggest that a soft-calling species like *H. pickersgilli* will most likely never match the power of low-flying aircraft noise and the noise generated by airplanes especially excludes species with quiet calls, and therefore, adaptations that assist the species in improving communication with potential mates are favored. The negative effects that anthropogenic noise might have on anuran behavior include impaired sender and receiver detection thresholds and spatial orientation, decreased breeding success, decrease of active distance of calls by masking effects of noise, distribution changes, changes in call temporal and spectral properties and sexual selection (Wiley 1994; Carr and Fahrig 2001; Wollerman and Wiley 2002; Brumm and Slabbekoorn 2005; Langemann and Klump 2005; Bee and Swanson 2007; Eigenbrod et al. 2009; Fahrig and Rytwinski 2009; Parris et al. 2009; Cunnington and Fahrig 2010; Hoskin and Goosem 2010; Kaiser et al. 2010; Herrera-Montes and Aide 2011). Although some frogs such as *Hyla arborea* are unable to adjust the frequency or duration of their calls to increase signal transmission (Lengagne 2008), the variation in call frequency exhibited by *H. pickersgilli* at a noise-polluted site should be incorporated in the description of the call of this species. The call description should consist of a good sample size in

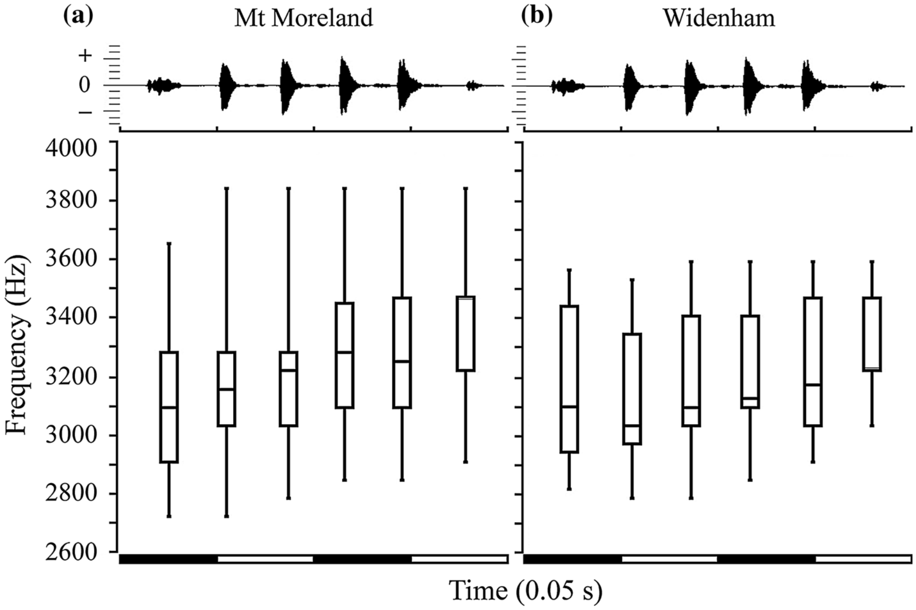

Fig. 7 Generalized oscillograms (*top*) and box plots showing call frequency analyses for each of six pulses of 10 calls ($n = 6$) from Mt Moreland (**a**) and Widenham (**b**). This shows variation in male call frequency in the population exposed to intense airplane flyby noise (**a**). Each box plot and associated mean represents the frequency band that the distinctive six pulses of the advertisement call of *H. pickersgilli* occupy. The *whiskers* indicate the maximum and minimum dominant frequencies. Note the greater variation in higher frequency bands of the airplane flyby noise exposed males (**a**)

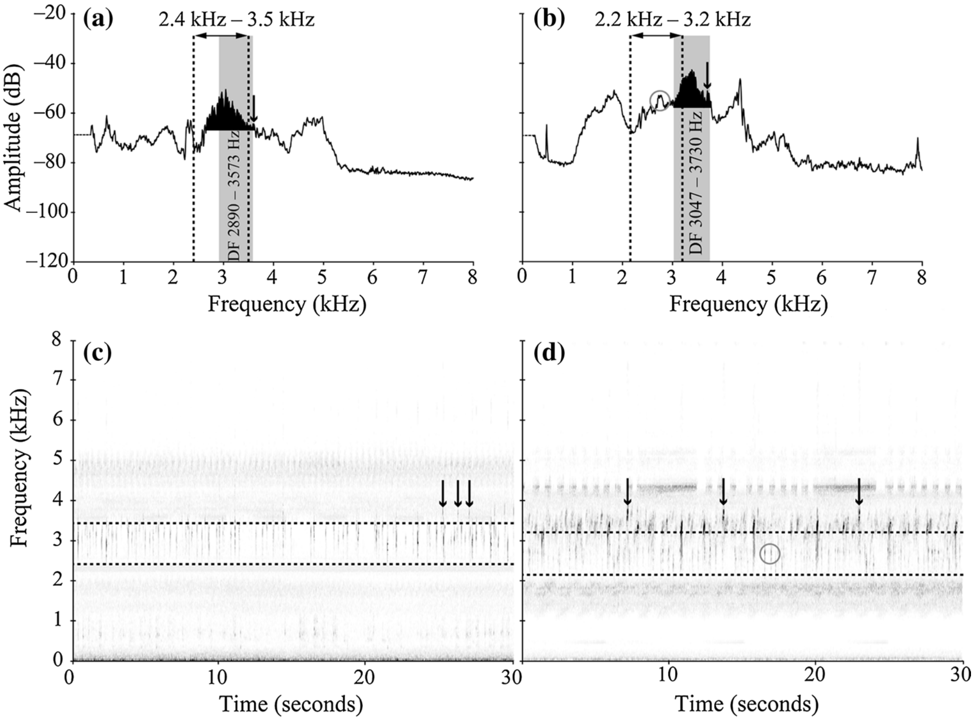

Fig. 8 Power spectra (**a**, **b**) and spectrograms (**c**, **d**) of 30-s soundscape recordings at the reference site, Widenham (**a**, **c**) and Mt Moreland on 11 November 2012, 03:00 am (at 15.8 and 16.3 °C ambient temperature, respectively). *Dashed lines* indicate an "open" acoustic niche devoid of background noise produced by insects. *Grey zones* in power spectra demarcate dominant frequency ranges of *Hyperolius pickersgilli* male advertisement calls at each site (Table 1). Filled power spectrum areas denote *H. pickersgilli* choruses on respective spectrograms, where arrows indicate male individuals calling at a higher frequency channel. Note the difference of the dominant frequency ranges between the two populations. *Grey circles* illustrate the position of *H. tuberilinguis* calls (**b**, **d**), a species occurring at both sites but not calling in the time-frame of the Widenham recording

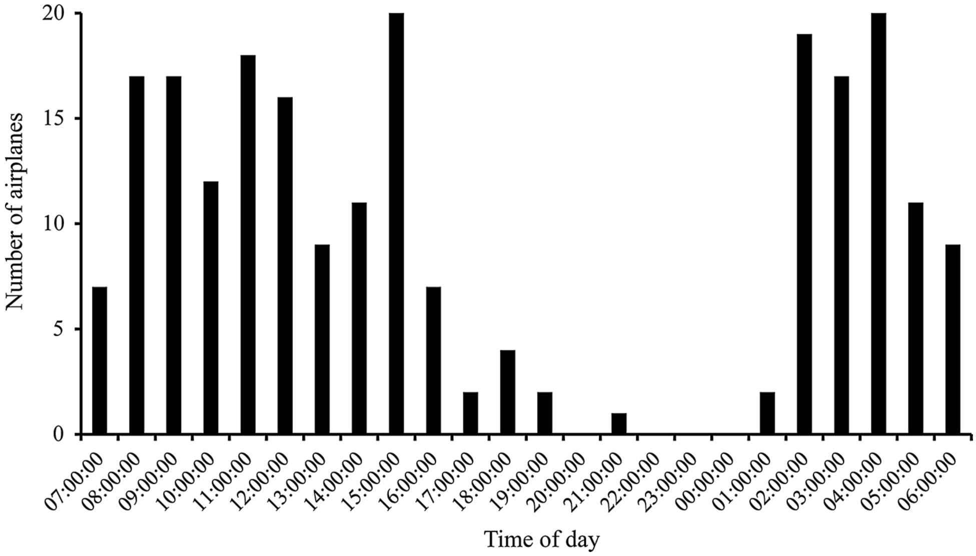

Fig. 9 Amount of airplane overflights per hour over Mt Moreland measured cumulatively over a period of 72 h in February 2013 ($n = 221$)

order to capture variation. Raw (1982) originally described *H. pickersgilli*'s call as having a "frequency intensity" of 3 kHz, but does not mention sample size.

Male and female frogs need to parse complex auditory input (specifically from inter- and intraspecific choruses) to make sense of the surrounding acoustic scene. This is achieved by overcoming two challenges, namely: auditory masking; and the perceptual binding spectral and temporal sound features containing an acoustic signal to generate a comprehensible auditory message (Bee 2012; Vélez et al. 2013). These challenges are overcome by separating signals from masking by "chorus-shaped noise", auditory grouping and/or auditory induction (see Bee 2012 for an elaborate review on these mechanisms in frogs). However, it is unclear if these mechanisms are sufficient in environments where anthropogenic noise is added to the auditory scene (Schwartz and Bee 2013). Furthermore, the strategy to signal louder as noise levels increase (termed the "Lombard effect") are not known to be exhibited by anurans (Love and Bee 2010). But, in a study conducted by Bee and Swanson (2007) to investigated its impacts on signal active space, single stimulus phonotaxis experiments with Cope's gray tree frog (*Hyla chrysoscelis*) revealed that traffic-shaped noise used masking conditions could enforce restrictions on communication in this species. However, whether anthropogenic noise creates a significant threat to anurans remains uncertain.

Limitations and future studies

Weather conditions play an integral part in chorus intensity of frogs (Lemckert et al. 2013). Due to the spatial separation of the two populations evaluated in this study, weather conditions could not have been controlled for due to the lack of empirical evidence on which variables affected calling intensity. Furthermore, empirical playback studies at the Widenham site (devoid of airplane noise) can provide a more controlled experiment and would further clarify whether this population will react to airplane noise in the same manner as did the Mt Moreland population. Due to the difference in response to anthropogenic noise by different species, more studies are needed to evaluate the effects thereof on frog behavioral ecology globally.

This study has demonstrated that an individual male's call can be followed throughout the evening due to males' fidelity to calling sites and the acoustic properties of a chorus, e.g. the varying amplitude and frequency of each male in a passive recording. Although it is not possible to identify a single male only by its call properties, the number of males calling in a specific time frame can be singled out and monitored throughout an evening chorus. Habitat fragmentation caused by urbanization and agricultural land expansion, may force *H. pickersgilli* to co-exist in closer proximity to other species and at higher densities, which will increase acoustic competition and may result in migration. This in turn may impact breeding success, resulting in local extinctions. In amphibian conservation it is crucial not to conserve small pockets of habitat, but rather to protect areas large enough with habitat corridors between breeding sites so that species can persist in the long-term (Bulman et al. 2007). However, *H. pickersgilli* occurs in already severely fragmented pockets of wetlands and are habitat specific (Tarrant and Armstrong 2013). Therefore, the highest priority should be given to conserving existing breeding populations. Acoustic interference should be assessed at these populations and monitoring programs introduced using passive acoustic monitoring. Furthermore, airplane noise playback experiments should be conducted at the reference site (Widenham) to investigate whether this population reacts in a similar way as the population at Mount Moreland.

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Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

References

Arch VS, Grafe TU, Gridi-Papp M, Narins PM (2009) Pure ultrasonic communication in an endemic Bornean frog. PLoS One. doi:10.1371/journal.pone.0005413

Barber JR, Crooks KR, Fristrup KM (2009a) The costs of chronic noise exposure for terrestrial organisms. Trends Ecol Evol 25:180–189. doi:10.1016/j.tree.2009.08.002

Barber JR, Fristrup KM, Brown CL, Hardy AR, Angeloni LM, Crooks KR (2009b) Conserving the wild life therein: protecting park fauna from anthropogenic noise. Park Sci 26:26–31

Bee MA (2012) Sound source perception in anuran amphibians. Curr Opin Neurobiol 22:301–310. doi:10.1016/j.conb.2011.12.014

Bee MA, Swanson EM (2007) Auditory masking of anuran advertisement calls by road traffic noise. Anim Behav 74:1765–1776. doi:10.1016/j.anbehav.2007.03.019

Blair WF (1974) Character displacement in frogs. Amer Zool 14:1119–1125

Boeckle M, Preininger D, Hödl W (2009) Communication in noisy environments I: acoustic signals of *Staurois latopalmatus* Boulenger 1887. Herpetologica 65:154–165. doi:10.1655/07-071R1.1

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sunderland (MA), Sinauer Associates

Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. Adv Stud Behav 35:151–209. doi:10.1016/S0065-3454(05)35004-2

Bucher TL, Ryan MJ, Bartholomew GA (1982) Oxygen consumption during resting, calling, and nest building in the frog *Physalaemus pustulosus*. Physiol Zool 55:10–22

Bulman CR, Wilson RJ, Holt AR, Bravo LG, Early RI, Warren MS, Thomas CD (2007) Minimum viable metapopulation size, extinction debt, and the conservation of declining species. Ecol Appl 17:1460–1473. doi:10.1890/06-1032.1

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of different vagility. Conserv Biol 15:1071–1078. doi:10.1046/j.1523-1739.2001.0150041071.x

SPSS IBM Corp (2013) IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp

Cunnington GC, Fahrig L (2010) Plasticity in the vocalizations of anurans in response to traffic noise. Acta Oecologia 36:463–470. doi:10.1016/j.actao.2010.06.002

Dowling JL, Luther DA, Marra PP (2012) Comparative effects of urban development and anthropogenic noise on bird songs. Behav Ecol 23:201–209. doi:10.1093/beheco/arr176

Drewry GE, Rand AS (1983) Characteristics of an acoustic community: puerto Rican frogs of the genus *Eleutherodactylus*. Copeia 1983:941–953. doi:10.1046/j.1461-0248.2003.00420.x

Du Preez L, Carruthers V (2009) A complete guide to the frogs of Southern Africa. Struik Nat, Cape Town

Eigenbrod F, Hecnar SJ, Fahrig L (2009) Quantifying the road effect zone: threshold effects of a motorway on anuran populations in Ontario, Canada. Ecol Soc 14:24. http://www.ecologyandsociety.org/vol14/iss1/art24/

Emerson SB (2001) Male advertisement calls: behavioral variation and physiological processes. In: Ryan MJ (ed) Anuran communication. Smithsonian Institution Press, Washington, pp 36–44

Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc 14:21. http://www.ecologyandsociety.org/vol14/iss1/art21/

Forrest TG (1994) From sender to receiver: propagation and environmental effects on acoustic signals. Integr Comp Biol 34:644–654. doi:10.1093/icb/34.6.644

Garcia-Rutledge E, Narins PM (2001) Shared acoustic resources in an old world frog community. Herpetologica 57:103–116

Gerhardt HC (1982) Sound pattern recognition in some North American treefrogs (Anura: hylidae): implications for mate choice. Amer Zool 22:581–595. doi:10.1093/icb/22.3.581

Gerhardt HC, Huber F (2002) Acoustic communication in insects and anurans: common problems and diverse solutions. University of Chicago Press, Chicago

Gerhardt HC, Schwartz JJ (1995) Interspecific interactions in anuran courtship. In: Heatwole H, Sullivan BK (eds) Social behaviour: amphibian biology, vol 2. Surrey Beatty and Sons, Chipping Norton, pp 603–632

Grafe U (1997) Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. Anim Behav 53:1103–1117. doi:10.1006/anbe.1996.0427

Hauser MD (1996) The evolution of communication. MIT Press, Cambridge

Herrera-Montes MI, Aide TM (2011) Impacts of traffic noise on anuran and bird communities. Urban Ecosyst 14:415–427. doi:10.1007/s11252-011-0158-7

Hoskin CJ (2004) Australian microhylid frogs (Cophixalus and Austrochaperina): phylogeny, taxonomy, calls, distribution and breeding biology. Aust J Zool 52:237–269. doi:10.1111/cla.12118

Hoskin CJ, Goosem MW (2010) Road impacts on abundance, call traits, and body size of rainforest frogs in northeast Australia. Ecol Soc 15:15. http://www.ecologyandsociety.org/vol15/iss3/art15/

Hoskin CJ, Higgie M, Mcdonald KR, Moritz C (2005) Reinforcement drives rapid allopatric speciation. Nature 437:1353–1356. doi:10.1038/nature04004

Hoskin CJ, James S, Grigg GC (2009) Ecology and taxonomy-driven deviations in the frog call-body size relationship across the diverse Australian frog fauna. J Zool 278:36–41. doi:10.1111/j.1469-7998.2009.00550.x

IUCN (2014) IUCN Red List of Threatened Species. Version 2014.2. www.iucnredlist.org. Accessed 6 March 2015

Kaiser K, Hammers JL (2009) The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, *Dendropsophus triangulum*. Behaviour 146:1053–1069. doi:10.1163/156853909X404457

Kaiser K, Scofield DG, Alloush M, Jones RM, Marczak S, Martineau K, Oliva MK, Narins PM (2010) When sounds collide: the effect of anthropogenic noise on a breeding assemblage of frogs in Belize, Central America. Behaviour 148:215–232. doi:10.1163/000579510X551660

Krause B (2004) The effect of low-level jet overflights on the natural soundscape. Presented at Natural soundscapes and noisy humans: a tale of two canyons. Palm Springs, California, Session IX, 3 March

Landon DM, Krausman PR, Koenen KKG, Harris LK (2003) Pronghorn use of areas with varying sound pressure levels. Southwest Nat 48:725–728. doi:10.1894/0038-4909(2003)048 < 0725:PUOAWV > 2.0.CO;2

Langemann U, Klump GM (2005) Perception and acoustic communication networks. In: McGregor PK (ed) Animal. Communication Networks Cambridge University Press, Cambridge, pp 451–480

Lemckert F, Penman T, Mahony M (2013) Relationship of calling intensity to micrometeorology in pond breeding frogs from central eastern New South Wales. Proc Int Acad Ecol Environ Sci 3:170–180

Lengagne T (2008) Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. Biol Conserv 141:2023–2031. doi:10.1016/j.biocon.2008.05.017

Love EK, Bee MA (2010) An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. Anim Behav 80:509–515. doi:10.1016/j.anbehav.2010.05.031

Mac Nally RC (1981) On the reproductive energetics of chorusing males: energy depletion profiles, restoration and growth in two sympatric species of *Ranidella* (Anura). Oecologia 51:181–188. doi:10.1007/BF00540598

Melcón ML, Cummins AJ, Kerosky SM, Roche LK, Wiggins SM, Hildebrand JA (2012) Blue whales respond to anthropogenic noise. PLoS One 7:e32681. doi:10.1371/journal.pone.0032681

Michelsen A (1978) Sound reception in different environments. In: Ali MA (ed) Sensory ecology: review and perspectives. Plenum, New York, pp 345–373

Narins PM (1982) Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). J Comp Physiol 147:439–446. doi:10.1007/BF00612008

NEMBA (2004) National Environmental Management Biodiversity Act 2004, Act No. 10 of 2004. Government Gazette, Cape Town

Parris KM, McCarthy MA (2013) Predicting the effect of urban noise on the active space of avian vocal signals. Am Nat 182:452–464

Parris KM, Schneider A (2009) Impacts of traffic noise and traffic volume on birds in roadside habitats. Ecol Soc 14:29. http://www.ecologyandsociety.org/vol14/iss1/art29/

Parris KM, Velik-Lord M, North JMA (2009) Frogs call at a higher pitch in traffic noise. Ecol Soc 14:25. http://www.ecologyandsociety.org/vol14/iss1/art25/

Penna M, Narins PM, Feng AS (2005) Thresholds for evoked vocal responses of *Eupsophus emiliopugini* (Amphibia, Leptodactylidae). Herpetologica 61:1–8. doi:10.1655/04-21

Pepper CB, Nascarella MA, Kendall RJ (2003) A review of the effects of aircraft noise on wildlife and humans, current control mechanisms, and the need for further study. Environ Manage 32:418–432. doi:10.1007/s00267-003-3024-4

Popper AN, Hastings MC (2009) The effects of anthropogenic sources of sound on fishes. J Fish Biol 75:455–489. doi:10.1111/j.1095-8649.2009.02319.x

Pough FH, Magnusson WE, Ryan MJ, Wells KD, Taigen TL (1992) Behavioral energetics. In: Feder ME, Burggren WW (eds) Environmental physiology of the amphibians. University of Chicago Press, Chicago, pp 395–436

Prestwich KN, Brugger KE, Topping MJ (1989) Energy and communication in three species of hylid frogs: power input, power output and efficiency. J Exp Biol 144:53–80

Rand AS (1985) Trade-offs in the evolution of frog calls. Proc Anim Sci 94:623–637. doi:10.1007/BF03191864

Raw LRG (1982) A new species of reed frog (Amphibia: Hyperoliidae) from the coastal lowlands of Natal, South Africa. Durban Mus Novit 13:117–126

Richards DG, Wiley RH (1980) Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. Amer Nat 115:381–399. doi:10.1086/283568

Schwartz JJ, Bee MA (2013) Anuran acoustic signal production in noisy environments. In: Brumm H (ed) Animal communication and noise, vol 2. Springer, New York, pp 91–132

Schwartz JJ, Gerhardt HC (1995) Directionality of the auditory system and call pattern recognition during acoustic interference in the gray treefrog, *Hyla versicolor*. Auditory Neurosci 1:195–206

Sun JWC, Narins PM (2005) Anthropogenic sounds differentially affect amphibian call rate. Biol Conserv 121:419–427. doi:10.1016/j.biocon.2004.05.017

Taigen TL, Wells KD (1985) Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). J Comp Physiol B 155:163–170. doi:10.1007/BF00685209

Taigen TL, Wells KD, Marsh RL (1985) The enzymatic basis of high metabolic rates in calling frogs. Physiol Zool 58:719–726. doi:10.1086/637593

Tarrant J (2012) Tapping into frog conservation: a new programme for the Endangered Wildlife Trust. African Herp News 58:1–3

Tarrant J, Armstrong AJ (2013) Using predictive modelling to guide the conservation of a critically endangered coastal wetland amphibian. J Nat Conserv 21:369–381. doi:10.1080/00063657.2013.849656

Vargas-Salinas F, Amézquita A (2013) Traffic noise correlates with calling time but not spatial distribution in the threatened poison frog *Andinobates bombetes*. Behaviour 150:569–584. doi:10.1163/1568539X-00003068

Vargas-Salinas F, Cunnington GM, Amézquita A, Fahrig L (2014) Does traffic noise alter calling time in frogs and toads? A case study of anurans in Eastern Ontario, Canada. Urban Ecosyst 17:945–953. doi:10.1007/s11252-014-0374-z

Vélez A, Schwartz JJ, Bee MA (2013) Anuran acoustic signal perception in noisy environments. In: Brumm H (ed) Animal communication and noise, vol 2. Springer, New York, pp 133–185

Wells KD (2007) Ecology and behavior of amphibians. The University of Chicago Press, Chicago

Wells KD, Taigen TL (1989) Calling energetics of a Neotropical treefrog, *Hyla microcephala*. Behav Ecol Sociobiol 25:13–22. doi:10.1007/BF00299706

Wiley RH (1994) Errors, exaggeration, and deception in animal communication. In: Real LA (ed) behavioral mechanisms in evolutionary ecology. University of Chicago Press, Chicago, pp 157–189

Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav Ecol Sociobiol 3:69–94. doi:10.1007/BF00300047

Wiley RH, Richards DG (1982) Adaptation for acoustic communication in birds: sound transmission and detection. In: Kroodsma DE, Miller EH (eds) acoustic communication in birds, vol 1. Academic Press, New York, pp 132–181

Wilkens MR, Seddon N, Saffran RJ (2013) Evolutionary divergence in acoustic signals: causes and consequences. Trends Ecol Evol 28:156–166. doi:10.1016/j.tree.2012.10.002

Wollerman L (1999) Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. Anim Behav 57:529–536. doi:10.1007/s11692-014-9274-7

Wollerman L, Wiley RH (2002) Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. Anim Behav 63:15–22. doi:10.1093/beheco/art125

Ziegler L, Arim M, Narins PM (2011) Linking amphibian call structure to the environment: the interplay between phenotypic flexibility and individual attributes. Behav Ecol 22:520–526